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Jay L. Lush
Iowa State College

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By Jay L. Lush

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R. M. Hughes, Acting Director

ANIMAL HUSBANDRY SECTION
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SUMMARY

Linebreeding is a form of inbreeding (usually mild) directed toward keeping the offspring closely related to one ancestor (usually a much admired one). All inbreeding not necessary for holding this relationship high is avoided as far as possible.

It is practiced to conserve, among the descendants, the good traits of an outstanding sire or dam, increasing those descendants in numbers without lessening their resemblance to this ancestor even for many generations after that ancestor's death.

The more superior a breeder's herd or flock is to the average merit of its breed, the more reason he has to practice linebreeding to his very best animals or to the very best of their recent ancestors. Breeders of grades cannot often afford to do much linebreeding.

The closeness of relationship and the intensity of inbreeding are presented in figs. 1 and 2 and table I for some of the more common types of mating related animals.

A breed can be improved most rapidly when at least its better herds are practicing linebreeding at about the rate which would occur if it were divided into isolated groups of herds with about 3 to 5 sires in each group.

Several plans are suggested whereby an individual may start on a linebreeding plan with some assurance that he will not have to give it up soon in order to avoid extreme linebreeding to ordinary ancestors.

All these plans involve cooperation with other breeders in some way or other except in those rare cases where a single herd is large enough to use economically three to five sires at all times.

The more meritorious the foundation stock is and the more skillful the breeder is in his selections, the more extremely he can linebreed with safety.

From the genetic point of view, linebreeding is a form of inbreeding devised to hold whatever has already been gained by selection while trying to make still further gains by additional selection. The selection practiced in linebreeding is aimed primarily at deciding which proved ancestors are to have their influence perpetuated.

There is no magic about the linebreeding process which will automatically produce good results. If selection is not practiced, a breeder would do well to avoid linebreeding altogether. But a breeder starting with good stock and directing the linebreeding toward the best of its recent ancestors can effect more improvement by selection while holding the improvement he already has than would be possible if he were continually outcrossing.

Linebreeding*

By Jay L. Lush

WHAT LINEBREEDING IS

Linebreeding is mating animals so that their descendants will be kept closely related to some animal regarded as unusually desirable. This is accomplished by using for parents animals which are both closely related to the admired ancestor but are little if at all related to each other through any other ancestors. The animal toward which the linebreeding is directed is usually named when a breeder describes a linebred pedigree. Thus a breeder will rarely say: ''This is a linebred bull.'' Such a sentence is scarcely complete. Instead he will say: ''This bull is a linebred Beau President'' or ''This bull is linebred to Black Woodlawn.''

Since both parents are descended from the ancestor toward which the linebreeding is being directed, they are related to each other and their mating is a form of inbreeding (in the broad sense of that word). Linebreeding possesses some of the advantages and dangers of other forms of inbreeding. But since the main object of linebreeding is to keep the offspring closely related to the esteemed ancestor, the breeder usually tries to avoid all inbreeding not necessary for this purpose. Hence linebreeding is usually less intense than other forms of inbreeding. Inbreeding is used above, as in scientific usage, to mean any mating of individuals more closely related than the average relationship within the population concerned. Practical breeders often restrict the word inbreeding to the very closest matings but differ about how closely related the mated animals must be before the mating is called inbreeding.

Linebreeding thus differs from other forms of inbreeding *primarily* in that it is always directed toward maintaining a high relationship to some chosen ancestor, and *secondarily* in that it is usually less intense than the most extreme inbreeding which might be practiced.

EXAMPLES OF LINEBREEDING

The illustrations on page 341 show the difference between linebreeding and other forms of inbreeding. The parents of X are ''double first cousins,'' having the same four grandparents. The parents of Y are half brother and sister.

Z is produced by mating a sire to his own granddaughter. The *intensity* of the inbreeding is the same for all three. But X would rarely if ever be called linebred. The relation between

* Project 33 of the Iowa Agricultural Experiment Station.

its sire and its dam comes through four different ancestors which they have in common and which, so far as the pedigree shows, may belong to four unrelated strains. Y is linebred to M because K and L are related only through M (as far as the pedigree shows) and Y has been kept about as closely related to M as its parents were. Z is even more clearly a case of linebreeding because it is more apt to be like M than Y is. All of the danger from inbreeding in producing Y and Z is the risk of uncovering and fixing undesired hereditary traits possessed by one animal—M. The danger from inbreeding in producing X is scattered among four different ancestors.

```
                G                                 
        C       H              M                M
    A           I          K
        D       J              N
X                     Y                    Z
        E       G              M                    Q
    B           H          L                    P
        F       I              O                    L   M
                J                                       O
```

If one ancestor has proved itself by its own performance and by the performance of its offspring to be outstanding among its contemporaries, we would naturally seek to perpetuate its traits by matings of the Y or Z type. If we ever did have a case where all the ancestors were about equally outstanding, we might proceed somewhat as in X but naturally that wouldn't happen often.

Another illustration may make the difference clearer.

```
                                            I
      M                             M       J
                                R           I
W                                   D       J
              M             V
      S                             M       I
              L     M           T           J
                    O               D       I
                                            J
```

W and V are each inbred so intensely that about 3/8 of the hereditary units normally unfixed (heterozygous) in their breed are probably fixed (homozygous) and prepotent in these two animals. Yet all the inbreeding in W is directed toward recovering and intensifying the traits of one ancestor (M) while the inbreeding of V is scattered equally between I and J or between their two offspring (M and D). Most breeders would call both animals "inbred" because the inbreeding is so intense, but some would call W "intensely linebred to M." Probably no one would call V linebred. Again in comparing the animals S and Z, some might prefer to call S "inbred" instead of linebred because, although all the inbreeding in both cases is directed toward M, yet the inbreeding of S is very intense (1/4 of the traits fixed). Others would call S "strongly linebred to M." All would call Z linebred because it conforms to both parts of the definition of linebreeding, the inbreeding not being extremely intense (1/8 of the traits fixed) and all of it being directed toward one ancestor. To be sure, S will probably be more like M than Z will, but the danger (inbreeding intensity) in producing S is twice as great, and most breeders would think that the moderate increase in likeness wasn't worth running an inbreeding risk double that involved in the production of Z.

WHY LINEBREEDING IS PRACTICED

Breeders practice linebreeding to hold together as long as possible and to keep in as pure a form as possible the good traits of a sire or dam which has been an unusually good breeding animal.

ANIMALS DO NOT LIVE LONG

When an animal has at last proved itself through its own performance and that of its progeny to have an unusually good inheritance, the breeder naturally wants to keep the good qualities of that animal and to spread them through his whole flock or herd. As long as it is alive, he can get sons and daughters from it. But often it will be old or even dead before its real superiority is recognized. In any event the time will come sooner or later when he can no longer get new sons or daughters from it. Moreover those sons or daughters have received only half of their inheritance from this one parent. The kind of individual each is and the way it breeds will depend also upon what it received from its other parent.

OUTCROSSING DIMINISHES AN ANCESTOR'S IMPORTANCE

When these sons and daughters are mated to unrelated individuals the offspring will get only about one-fourth of their inheritance from their outstanding grandparent. If they in turn are mated to unrelated individuals, the influence of the outstanding ancestor is again halved or "diluted." If its descendants are continually bred to unrelated animals, it will be only three or four generations until this one ancestor's influence is so "diluted" that it becomes unimportant, as far as its probable influence on any one descendant is concerned.

INHERITANCE IS A SAMPLING PROCESS

A parent gives to each one of its offspring a sample half of all the inheritance it has. Since these are samples and not uniform blends of the parent's inheritance, and since the total inheritance is made up of an enormous number of different units, a parent may have many different offspring without ever giving any two of them exactly the same sample from its inheritance.

P (in the pedigree of Z, page 341) gets half her inheritance from Q and half from L. The half she gets from L is a sample partly of what L received from M and partly of what came to L from O. Theoretically the inheritance which L transmits to P can vary all the way from being entirely from M to being entirely from O. And this extreme variation actually occurs, if attention is confined only to single traits, simple in their inheritance. The practical breeder, however, must consider the animal as a whole with all its traits. There are so many different units in its total inheritance that the sample it transmits will usually be about half from its sire and half from its dam. This will be nearly true even for any one son or daughter and will be almost exactly true for the average of what it transmits to all its offspring. Z gets half its inheritance from M directly and about $\frac{1}{4}$ of the half it receives from P will be from M originally. Hence about $\frac{5}{8}$ of Z's inheritance is from M and we would naturally expect Z to be more like M than an ordinary son or daughter would be.

If M is still alive when we come to realize that he really is a great sire, we may very well linebreed to him as was done in producing Z. If M is dead by the time we realize how good a sire he was, a mating of the kind illustrated by Y's pedigree will help keep M's influence from being further diluted and scattered, but will not produce animals any more closely related to M than the most closely related living descendant is when the linebreeding is begun. Y gets about one-fourth of its inheritance from M through K and about another fourth from M through L, making about half from M in all. Theoretically it can vary all the way from having nothing from M to having all its inheritance from M, but in actual practice neither extreme would happen once in many millions of cases if we consider the total inheritance for all different traits. Nearly all animals with pedigrees like that of Y would have received *about* half of their inheritance from M.

LINEBREEDING INCREASES PREPOTENCY

Linebreeding also builds up prepotency and uniformity within the herd where it is practiced, just as other kinds of inbreeding do. (Prepotency is the ability of a parent to impress its characteristics on its offspring more uniformly than the average parent can.) These are additional reasons for practicing linebreeding, but they are subordinate to the main purpose of conserving the good traits of a really great sire or dam long after it is dead. By linebreeding to this ancestor the breeder can multiply its descendants without lessening very much their resemblance to this ancestor.

WHO SHOULD PRACTICE LINEBREEDING?

Those who can best afford to consider linebreeding are breeders of purebreds whose herds or flocks are already distinctly superior to the general average of their breeds. Among these, it is particularly those who have been fortunate enough to have used for a time one of the really outstanding sires or dams of the breed, who ought to linebreed to that animal before it is too late.

LINEBREEDING NOT OFTEN ADVISABLE IN GRADE HERDS

Breeders of grades cannot often afford to linebreed. The inbreeding risk involved is just as great for them as it is for the breeder of purebreds. If they practice linebreeding and are successful, they cannot sell at a premium the increased prepotency and uniformity which will be put into their animals by the linebreeding. They risk losing as much (by the outcropping of defects most of which would remain hidden if no inbreeding were practiced) as the breeders of purebreds do, but do not have the chance to gain as much by successful linebreeding. Probably the only time the breeder of grades can afford to linebreed is when, by wise choice or lucky accident, he has used a sire whose offspring prove him to have been one of the truly outstanding sires of his breed. Cases of this kind do happen and on the whole it seems *likely* that there are more breeders of grades who lose by failing to conserve a good sire than there are who lose by getting too many of the usual bad results of inbreeding in their herds while trying to linebreed to a good sire. Nevertheless, as a general rule, a breeder of grades needs better reasons for linebreeding than a breeder of purebreds does. That is to say, the *certain merit* of the animal to which he might linebreed needs to be farther above the *probable merit* of the next sire which he would otherwise use, in the case of the breeder of grades than in the case of the breeder of purebreds.

LINEBREEDING IN PUREBRED HERDS OF AVERAGE MERIT

It is an open question whether the owner of an *average* purebred herd should practice any linebreeding. Certainly every such herd contains much good inheritance scattered among different animals. That inheritance won't have much chance of being brought together in a form pure enough that it can be selected effectively for further breeding unless linebreeding is practiced. Yet it is equally certain that linebreeding will bring to light hidden inheritance of the ancestors toward which it is directed. Hidden (recessive) inheritance tends generally to be less desirable than that (dominant) which is manifested even when it comes from one parent only. This is one reason for the degeneration which is the *usual* result of extreme and long-continued inbreeding of any kind.

If many breeders with herds of average merit were to practice linebreeding, a certain amount of inbreeding degeneration would be sure to come to light. This would differ from herd to herd, some showing more than others and probably no two changing in exactly the same way. It is *possible* that the increased effectiveness of selection when linebreeding is practiced would more than offset that average amount of inbreeding degeneration, but this is not certain.

All that can be said at present is that the more superior a herd is to the average merit of its breed, the more reason there is to practice linebreeding in that herd.

MEASUREMENT OF DEGREES OF LINEBREEDING

The two aspects of linebreeding—its direction and its intensity—are measured separately. Exact measures are rather complicated. They and certain rough estimates which will do well enough for most practical purposes are discussed in the Appendix.

In the following table and in figs. 1 and 2 are shown the relationships and the intensity of the inbreeding from a few of the commoner types of inbreeding or linebreeding matings.* The symbols are: F_x = the intensity of the inbreeding of animal X. R_{xy} = the relationship or probable likeness between the heredity of animal X and that of animal Y. The figures for intensity of inbreeding may be understood best by comparing them with 25 percent which results from one generation of parent x offspring or full brother x sister mating, or with 12½ percent which results from one generation of half brother x sister mating, or with 6¼ percent which is the result of first cousin matings (two grandparents in common, as in human first cousins). If the inbreeding is continued generation after generation, its intensity can approach 100 percent as a limit, but can never quite reach that. The closest inbreeding possible with animals requires three generations to reach 50 percent. Inbreeding coefficients much higher than 25 percent are unusual among the pedigrees encountered in practical animal breeding.

* If interested in a pedigree not adequately described here, write to the Animal Breeding Subsection of the Agricultural Expriment Station about it.

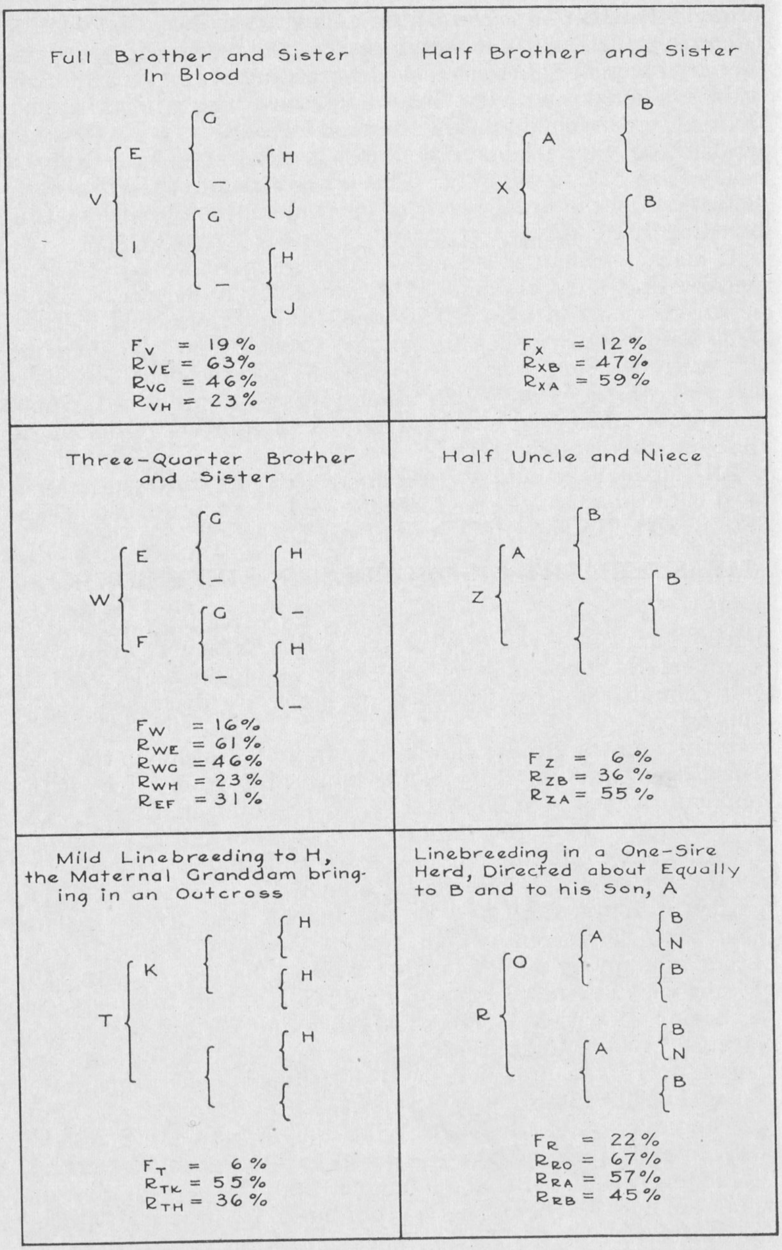

Fig. 1. Examples of linebreeding or mild inbreeding frequently seen in livestock pedigrees.

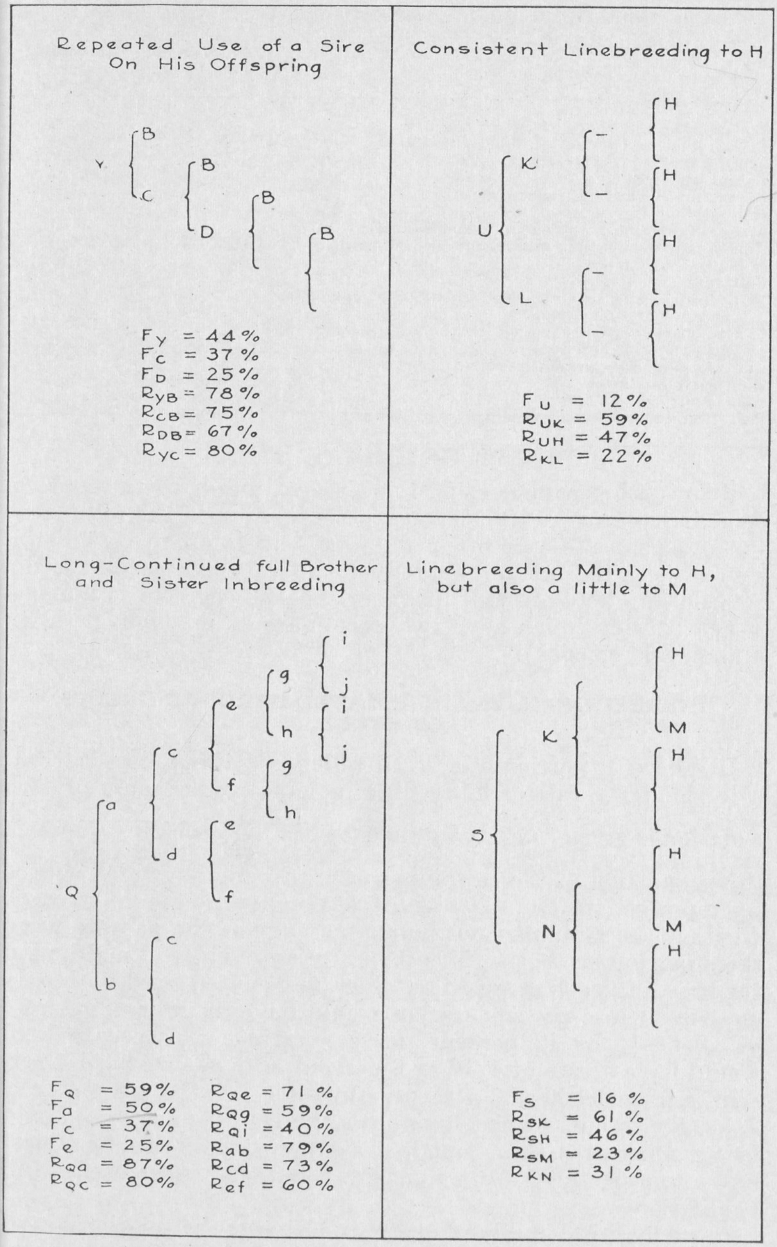

Fig. 2. Examples of long-continued linebreeding and inbreeding.

TABLE I. INBREEDING OR LINEBREEDING MATINGS COMMONLY FOUND

Kind of mating	Relation of mates to each other	Inbreeding of offspring
Full brother and sister (first generation)	50 %	25 %
Full brother and sister (second generation)	60 %	37½%
Full brother and sister (third generation)	73 %	50 %
Parent and offspring (first generation)	50 %	25 %
Parent and offspring (second generation)	67 %	37½%
Half brother and sister Grandparent and grandson or granddaughter Double first cousins (4 grandparents in common) Full uncle and niece Full aunt and nephew	25 %	12½%
"Full brother and sister in blood" (i.e. by the same sire and out of full sisters)	37½%	18¾%
"Three-quarter brother and sister" (i.e. by the same sire and out of half sisters)	31¼%	15⅝%
First cousins (two grandparents in common) Half uncle and niece Half aunt and nephew	12½%	6¼%
Half first cousins (one grandparent in common)	6¼%	3⅛%

Relationship cannot exceed 50 percent unless there has been some inbreeding. Fifty percent is the relationship of full brothers and sisters to each other and of parent to offspring in pedigrees where there is no inbreeding. Twenty-five percent is the relationship between half brothers and 12½ percent is that between cousins which have two grandparents in common (as in human first cousins).

INBREEDING RATES IN ISOLATED HERDS OR GROUPS OF HERDS

In a herd or portion of a breed which is entirely closed to outside blood, the rate of inbreeding inevitable on account of such isolation is given roughly by the formula $\frac{1}{8N}$ which represents the proportion of the remaining unfixed heredity which will be fixed per generation. The length of a generation is the average (neither the minimum nor maximum) age of the parents when the offspring are born. N is the effective number of males used for breeding each generation. Such an isolated herd with only one sire in use per generation would have an inbreeding rate of about ⅛ or 12 percent per generation. A two-sire herd would have a rate of 1/16 or 6 percent, a three-sire herd 4 percent, a four-sire herd 3 percent, a five-sire herd 2½ percent, etc. A herd with but one sire in use at a time but that sire used only half a generation (or a fourth of a generation) would be almost like a two-sire herd (or a four-sire herd) with sires used a full generation.

In such an isolated herd or group of herds the relationship of the descendants to the foundation animals would quickly stabilize at a certain level from which further breeding within that group could change it only by the (usually) slow process of selection for individual traits. For example, few "straight-bred" Anxiety 4th cattle today are related to Anxiety 4th less than 20 percent or much more than 32 percent, or to North Pole much less than 15 percent or more than 22 percent. It is not now possible by any system of breeding to produce cattle more closely related to either of these two Hereford sires than the larger of these figures. That would have been possible while they or their sons or daughters or double grandsons and double granddaughters were still alive, but all those are long since dead and the opportunity for extreme "concentration of this blood" has passed forever. It is still possible to breed Herefords with lower relationship to these two sires than the smaller figures stated, but one must go outside the limits of the "straight-bred" Anxiety 4th Herefords to do so.

IDEAL BREEDING SYSTEMS

Any ideal breeding system calls first of all for as effective use of selection as is possible. This naturally starts with as rigid selection of the individual animal as is compatible with paying attention also to the merits of the animal's parents, grandparents and other immediate relatives. When an animal can be judged by its progeny, that should take first place, but the initial choices of breeding animals must be made before they have any progeny. Any selection directed toward more than one point needs must compromise often. The most desirable individual in a particular group may not be out of the most desirable parents. We may have to choose the second or third best individual, in order also to get one whose parents are near the top. Even then, when the progeny come we will be forced to admit that in some cases the animal prized most highly for individuality and pedigree proved to be less desirable as a breeder than others which we had rated lower in the pedigree and individuality scale. Nevertheless, selection, using every possible basis for rating animals all through their lives, is the foundation of all breed improvement. The effectiveness of such selection may be increased greatly by combining it with a linebreeding system which will help hold what is gained by the successful selection.

An ideal breeding system for the most rapid improvement of the breed as a whole (leaving in the background for the moment the question of whether it would be most profitable for the breeders' personal fortunes), would be about as follows: Each breed would be divided into many small groups, each such group raising both its own males and females for the next generation, rarely introducing any breeding animals from other groups and then only with great caution. Each group should be about large enough for the use of three to five breeding males at all times and of course would include a much larger number of females. If the groups were much smaller than this, the rate of fixation on account of the inevitable inbreeding would probably be too high for selection to keep it under control. If the groups were much larger than this, progress toward uniformity within each group and toward distinctness from group to group would be needlessly slow.

The consequence of such a separation into groups, each breeding very largely within itself, would be (1) that each such group would quickly become more uniform than herds are today and (2) that each group would become different from other groups. Breeders could then know, more certainly than they do now, the kind of heredity their animals really have. Selection between groups would be effective to a degree impossible today.

Many of these groups would begin to show undesired traits varying in severity. Side by side with these they would show other highly desirable traits more uniformly than present herds do. Groups showing many desired and few undesired traits would make mild outcrosses to groups which were strong where they themselves were weak. If these outcrosses were successful, they would by renewed linebreeding with close selection attempt to fix the introduced desired traits without losing the desired traits they already had. If the outcrosses were not successful they would be discarded. Groups showing few desired and many undesired traits would either be discarded altogether or would be graded up by the continued use of sires from the most successful groups, until their individual merit was restored or even exceeded that of the most successful groups. Then they would begin renewed breeding within the group to find and fix the most desirable new combination of traits. The general rule would be that the more successful each group was, the less readily would it do any outcrossing and the milder such outcrossing would be.

The ideal system described here differs from the actual system of the past in that it calls for the maintenance at all times in each breed of *many such lines* or groups (instead of one or two) in various stages of formation and various stages of experimenting with mild outcrosses. It also requires that the linebreeding be carried farther than it has been in the past. If the real nature of the linebreeding process comes to be generally understood, as it doubtless will during the next decade, this should not lead to such fierce factionalism within the breed as would have been the case before 1920, when nearly all breeds were expanding rapidly and breeders were battling with each other over an exploitive stage of new business.

In the past, few breeders have been practicing much linebreeding at any one time. When a moderately successful line has arisen, there have usually been no other contemporary lines with which to compare it and toward which to make tentative mild outcrosses. Likewise, because of the commercial opportunities in exploiting those lines and because the real nature of linebreeding was not understood, there has often been a tendency to go to extremes. Enthusiasts have lauded the merits and denied the comparatively few but nonetheless real defects of the animals belonging to the popular line and have denied that much real merit existed outside the limits of the line. This has sometimes been carried to such absurd extremes of speculation in pedigrees that, since the nature of the linebreeding process was not understood, the whole linebreeding idea was often discredited lock, stock and barrel, in the eyes of saner breeders when the inevitable reaction came.

PLANS FOR INDIVIDUAL LINEBREEDING

A breeder whose herd is large enough that he can economically maintain in service at all times 3 to 5 different sires needs little active cooperation from other breeders. He can almost go his own way and work out his own ideas. But not many breeders have herds this large.

LINEBREEDING BY COOPERATION WITH COMMERCIAL BREEDERS

A breeder who uses but one or two sires at a time and keeps each in service only half a generation or less could get along by himself, but would be handicapped by not being able to use proved sires. They would be gone from his herd and probably dead before they were proved. Such a breeder can carry out a linebreeding program without much active cooperation from other breeders of purebreds if he can always sell a half interest in or lease a sire he is just through using. If that sire's offspring should prove him to have been an unusually good sire, he may still be alive and can be brought back for further use. Such a breeder would be using the cooperation of commercial breeders or breeders of grades to keep his sires for him until they were proven. In purebred cattle and sheep the average interval between generations is a little more than 4 years, in hogs a little less than 3 years. A dairy breeder might raise his own bulls, using each only a year before selling a half interest or leasing him. The next bull, being at least a year old at the time, would have been sired by the second or third preceding bull and would rarely be used on a dam or full sister. A few of the cows would be his half sisters, some would be cousins, and others would be still less closely related to him. The average rate of inbreeding would be about that of a three-sire or four-sire herd.

Occasionally a former sire would be brought back for further service after he had been away some 3 or more years. About a quarter of the herd would be his daughters, another quarter (or less) would be his granddaughters. A few of his half sisters might still be there. Hence the inbreeding of the resulting calves would average a little higher than usual, but that would be a risk worth taking since such a sire would be brought back only when his offspring had proved him to be an unusually good sire.

Such a plan would give a breeder the privilege of linebreeding to his best cows or bulls without making the rate of inbreeding dangerously high and without much formal cooperation with other breeders of purebreds. It would cost him the expense of rearing at all times at least one bull calf (more than one, if he wants the privilege of selecting between them on their own individuality before putting them in service). It may alienate from him the sympathy and cooperation of other leading breeders who may feel that such a separately directed breeding program is not cooperation with them at all. It may cause a few customers to turn away from his herd because it has the reputation of being closely bred. Both of these last objections will diminish in importance as the nature of the linebreeding process becomes better known, and as the value of the prepotent inbred sire in the production of grade or commercial animals becomes better known. Nevertheless these are real points to be considered before embarking on a linebreeding program. Is the privilege of linebreeding to his very best cows and bulls worth these costs? Naturally that depends on how much better those cows and bulls are than the average of their breed. That brings us back to the fundamental principle that the better a breeder's animals are, the more reason he has for linebreeding to the best among them.

MUTUAL COOPERATION BETWEEN SEVERAL BREEDERS WITH SMALL HERDS

Several breeders, each with a small herd, may linebreed by exchanging sires or, if they do not care to use old sires, each can arrange to get his next young sire out of one of the best dams in one of the other herds. This cuts down the expense and permits each to enjoy the cooperation of a few fellow breeders, but will still tend to isolate them from the rest of the breed. There should be 3 to 5 active breeders in such a cooperative arrangement in order to be sure to keep the inbreeding within safe limits. On account of economic vicissitudes which will cause some breeders to disperse their herds, probably such a group should plan to include 5 to 7 herds so that there would always be at least 3 to 5 herds actively continuing the plan.

Bull circles lend themselves very well to this form of cooperative linebreeding in dairy cattle where it is especially desirable that a supposedly good sire be kept in service at least 4 years until his real worth can be established by his daughters' performance. The members (usually 3 to 5) of a bull circle exchange sires every 2 years to avoid close inbreeding and, if the cows are good purebreds, the young bulls needed for replacement as the old bulls die or are culled, might very well come from the circle herds themselves.

LINEBREEDING IN HERDS LARGE ENOUGH TO KEEP TWO SIRES IN USE

Many a breeder can maintain a two-sire herd economically. By avoiding inbreeding as far as possible within those limits he can linebreed without formal cooperation from other breeders. This involves the fixation of nearly 6 percent of the still unfixed traits, both good and bad, per generation. Can selection be effective enough under those conditions to discard those animals in which undesired traits become fixed and to retain those in which the desired traits are fixed or at least are still present so that they have a chance to become fixed in future generations? The answer depends not only on how skilled the breeder is in making his selections and how much use he can make of progeny tests, pedigree estimates, etc., but also on how many undesirable bits of inheritance there are in the foundation stock. For things fairly simple in their inheritance and not much affected by environment, as for example details of color or distinct differences in skeletal shapes or proportions, even somewhat slack and careless selection ought to be enough to ward off undesired fixation. Undesired traits much affected by environment and complicated in their inheritance, as for example low fertility in swine or small size or low vigor in general, might drift into fixation even in the face of the strictest selection against them by the most careful breeder. Even a clumsy man can juggle 2 or 3 apples in the air without letting them fall and a fairly skillful juggler can handle 8 or 9, but the most skillful juggler in the world probably couldn't keep control of 30 or 40 at once.

Perhaps selection can control a fixation rate of 6 percent per generation if the foundation stock is unusually free from defects, either evident or hidden, and if the breeder in charge is unusually skillful in his selections. At any rate, here and there breeders are trying such plans.

TENTATIVE LINEBREEDING FOR ONLY ONE OR TWO GENERATIONS

Any breeder can linebreed at almost any time to some living or recently dead animal he admires. He can get along for a generation or two without cooperation in this. But if he is the only man breeding this line, and has not used some of the plans outlined above, he will soon come up against the fact that no one else has any animals closely related to his chosen foundation animal. The animals he breeds himself are so closely related to each other, through still other and more recent ancestors, that to use a sire of his own raising would be inbreeding more closely than he dares. He would be linebreeding to several other ancestors almost as much as to the chosen one. A linebreeding program which is to avoid this difficulty must prepare for it in advance by some plan like those suggested above. For example, until near 1925 it would have been fairly easy for anyone linebreeding to Black Woodlawn to go out among the Aberdeen Angus herds of Iowa and buy a new sire containing at least 25 percent and perhaps as much as 50 percent of the blood of Black Woodlawn and yet practically unrelated through other ancestors to the herd on which it was to be used. Today, for one reason or another, those herds have been dispersed or outcrossed with distantly related sires of more highly advertised bloodlines until such a breeder would have only a limited range for choosing a sire carrying even as much as 25 percent of the blood of Black Woodlawn.

When a breeder starts linebreeding to a noted sire or dam, that is usually a popular animal and he finds other breeders doing the same thing. Fashion in pedigrees, however, changes rapidly, especially under the impact of high-powered advertising campaigns and, even in the day when many are cooperating with him in linebreeding to this animal, he needs to be planning what he will do when he is almost alone in this purpose.

LINEBREEDING PURELY TO ONE ANCESTOR ALONE CANNOT BE CONTINUED INDEFINITELY

Linebreeding starts with an attempt to maintain at a high level the relationship of future animals to one ancestor. This can be done easily for two or three generations. If the linebreeding is continued, the time comes when further linebreeding also involves linebreeding to some of the descendants of that original ancestor. One may have saved several different sons and many different daughters of the noted ancestor, but sooner or later he will find that each of the descendants is descended from all or nearly all of these sons and daughters. Then these descendants cannot be mated together without also linebreeding to some of those sons and daughters. Moreover, even though several sons and daughters are saved, time is certain to prove some of them superior to the others. In the culling which accompanies any breeding program, more of the descendants of some sons and daughters than of others will be kept. This leads to some secondary linebreeding to certain sons and daughters. This may in time become even more intense than the linebreeding to the original ancestor. If one wishes to linebreed purely to one animal, he must see to it first of all that a very large number of sons and daughters of the esteemed ancestor are saved.

There is no particular reason why this secondary linebreeding should be avoided, provided the animal toward which it is directed is an unusually good one. The trouble is that if there are only a few different individuals in each generation it is likely to happen that in some generations no one of the few will be outstanding enough to justify linebreeding to it. If the number of animals in this linebred strain or family is very small, the breeder will have to linebreed to some of those, even though they have not proved themselves good enough to justify it. This is the intrinsic danger of a permanent linebreeding policy based on too small a herd. If the herd is large enough, such secondary linebreeding can be avoided or at least can be kept so small in amount in those generations when there is no one outstanding animal, that it will be practically harmless. This cannot be done in too small a herd.

CORRECTING DEFECTS IN A LINEBRED HERD BY OUTCROSSING

At any rate, defects which do become fixed usually disappear in the first generation of an outcross. This happens because of the generally recessive nature of undesired traits. Hence a line which does get some undesired trait fixed on it by the linebreeding, is still useful for outcrossing in the production of commercial stock. Or the breeder can outcross to other purebred stock and if the defect disappears in the first generation he can renew his linebreeding, using this outcrossed stock with the hope and real chance of fixing the corrected condition. The undesirable consequence of making an outcross is that it will also unfix some of the desirable inheritance which had already been fixed, particularly if the outcross is a very wide one. Hence much of the linebreeding will have to be done over again after each outcross.

EXAMPLES OF SUCCESSFUL LINEBREEDING

Figures 3 to 11 show actual pedigrees illustrating kinds of linebreeding. Most of these are pedigrees of modern animals reasonably successful as individuals. One could no doubt find similar pedigrees of distinctly unsuccessful animals. These pedigrees are so drawn that each ancestor's name appears but once. If it had more than one son or daughter in the pedigree, an additional arrow shows that line of descent.

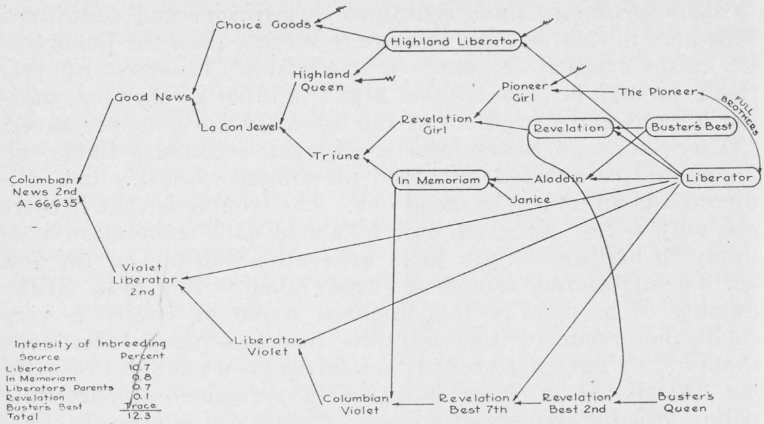

Fig. 3. Consistent linebreeding in a Poland China pedigree.

The pedigree of Columbian News 2d (fig. 3) shows almost pure linebreeding to Liberator, but there is a little to Revelation, In Memoriam, Buster's Best and to Liberator's parents. Violet Liberator 2d is consistently but very intensely (35.9 percent) linebred to Liberator. Mating her to Good News was a mild outcross because, while Good News traces four times to Liberator, yet he is not as closely related to Liberator as Violet Liberator 2nd was.

The Jersey pedigree (fig. 4) shows linebreeding originally directed toward the bull Financial King but recent descendants, such as Financial Superior, Financial Countess Lad and others actually contribute more to the total intensity of the inbreeding in the pedigree than Financial King does. The re-

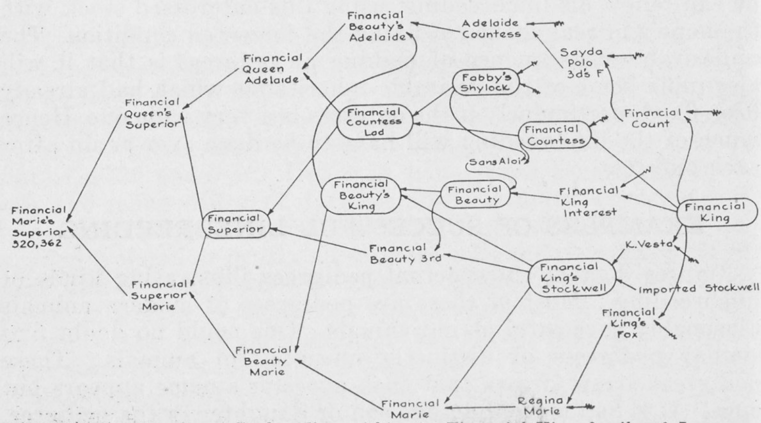

Fig. 4. Long-continued linebreeding within the Financial King family of Jerseys.

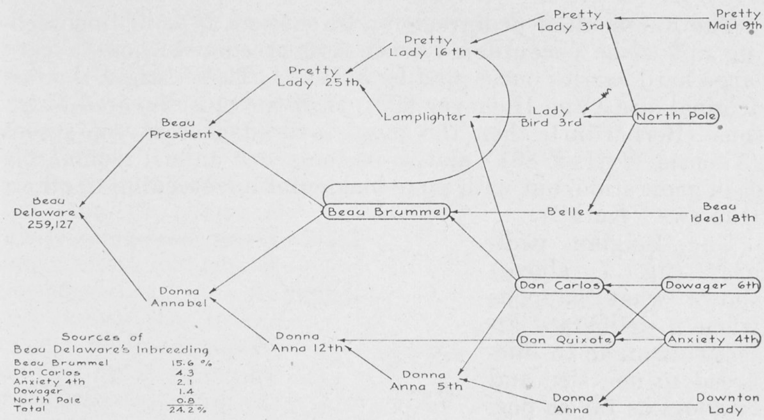

Fig. 5. A "straight-bred" Anxiety 4th Hereford. All lines go to daughters of North Pole or to sons or daughters of Anxiety 4th.

lationship to Financial King is maintained at about the same level as if he were a grandsire although he is five generations back in the nearest line.

The Hereford pedigree (fig. 5), although called an Anxiety 4th pedigree, shows more linebreeding to Beau Brummel and to Don Carlos than to Anxiety 4th himself. There is also some linebreeding to North Pole and to Dowager 6th. All or nearly all of the so-called "Straight bred Anxiety 4th" pedigrees of today hold the relationship of the present day animals higher to Beau Brummel and to Don Carlos than to Anxiety 4th, from which the family takes its name.

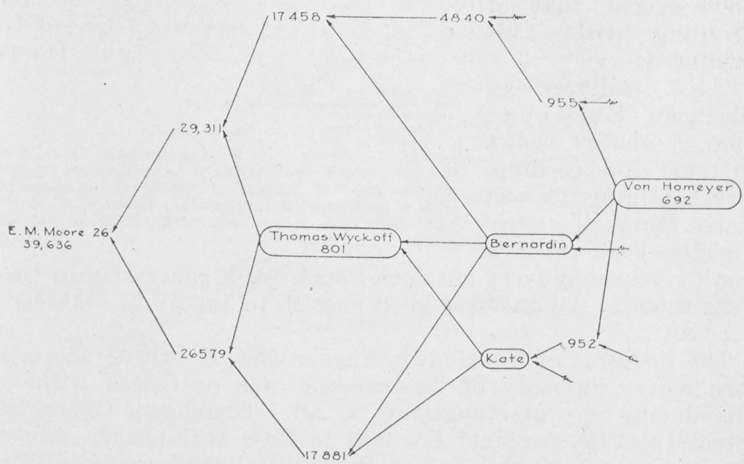

Fig. 6. A Rambouillet pedigree showing consistent linebreeding to one sire, his son and his grandson.

The Rambouillet pedigree (fig. 6) shows a type of linebreeding apt to be encountered when one breeder without a very large herd carries out a plan by himself. There is first a noted original sire (Von Homeyer 692), then the most favored of his sons (Bernardin), then the most favored of that son's sons (Thomas Wyckoff 801) and so on, only one animal dominating each generation, but with some incidental linebreeding to others (the ewe "Kate").

The Belgian pedigree (fig. 7, above) shows what happens when a deliberate attempt is made to linebreed to one sire and to avoid as far as possible linebreeding to any of the other ancestors, but necessarily operating in a stud of limited size. The Shorthorn pedigree (fig. 7, below) is one produced under much the same conditions as the Belgian pedigree, but with the breeder not following such a definite preconceived plan except that of breeding within his own herd.

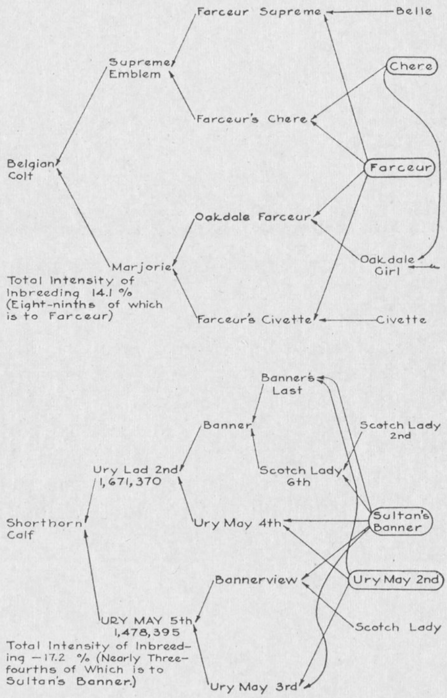

Fig. 7. Above: A Belgian pedigree in a two-sire herd where linebreeding is being directed toward maintaining "50 percent of the blood" of Farceur with a minimum of inbreeding. Below: A Shorthorn calf from a two-sire herd closed to outside blood.

The pedigree of Blackcap Empress (fig. 8, above) shows extreme linebreeding, directed purely toward Earl Marshall. Any breeder even with a small herd could carry out such a plan for a generation or two if he thought the ancestor good enough to justify the inbreeding risk.

The pedigree of Tomahawk Anchor (fig. 8, below) shows a case where intensity of linebreeding was decreased without introducing any new ancestors at all. Tomahawk Cherry is intensely (37½ percent) linebred to Rose Hill Larry. When she was mated to the sire of Rose Hill Larry, the resulting Tomahawk Anchor is linebred less strongly (22 percent) and all of this linebreeding is directed toward Rose Hill Anchor. Tomahawk Anchor's relationship to Rose Hill Anchor is 65 percent (all direct) and to Rose Hill Larry is 62 percent (more than a third of it being collateral).

The pedigree of Rabban (fig. 9) shows a fairly common type of linebreeding which is consistent but never very intense. The rather steady linebreeding to one family is offset by the continued introduction of a small amount of "new blood." One of Rabban's grand-dams, Elga Elliott 29th, is quite unrelated to the grandsire or to the other granddam for at least four generations farther back in the pedigree. Rabban himself is a double grandson, his dam is a double granddaughter, and his

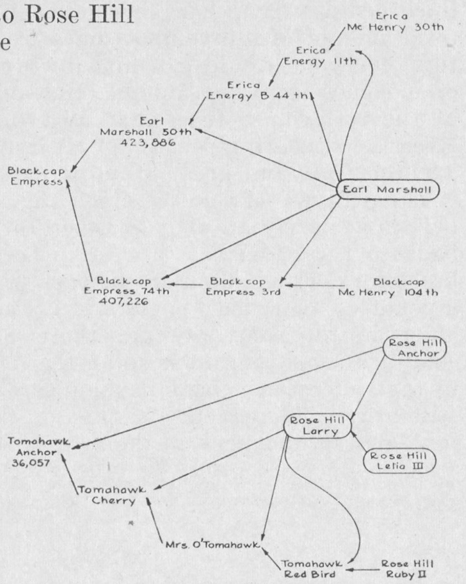

Fig. 8. Above: An Aberdeen Angus pedigree showing very extreme and consistent linebreeding to Earl Marshall. Below: A Tamworth pedigree showing consistent and fairly close linebreeding to Rose Hill Anchor, although the dam was more intensely and just as consistently linebred to a son of Rose Hill Anchor.

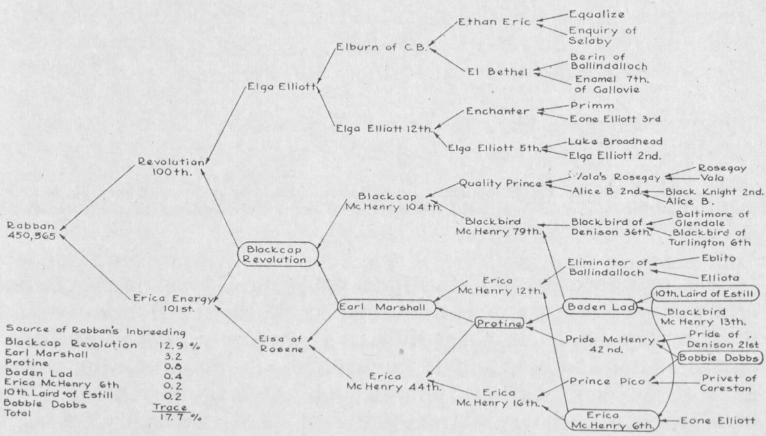

Fig. 9. An Aberdeen Angus pedigree showing consistent linebreeding in one family, generation after generation, but always accompanied by a little outcrossing, so that the total intensity never becomes very high.

maternal granddam is a double granddaughter. Yet there is enough outcrossing at every level in the pedigree to keep the linebreeding from ever becoming intense. While Rabban's total amount of inbreeding comes from several different ancestors, everyone would call him linebred since nearly four-fifths of it comes from one animal (Blackcap Revolution) and most of the rest comes from that ancestor's sire (Earl Marshall). Even the scattering remainder comes from Earl Marshall's sire, grandparents and great grandparents.

The pedigree of Good Fashion (fig. 10) shows consistent linebreeding, nearly all of it to Liberator, but all of it a long way back in the pedigree. For all practical purposes if the linebreeding does not show in the first three or four generations of a pedigree, there isn't enough of it that the breeder need worry about its intensity, although there may still be enough to accomplish something in keeping the descendants closely related to that ancestor. Good Fashion's relationship to Liberator is still nearly 33 percent in spite of Liberator's being at least four generations back in the nearest line.

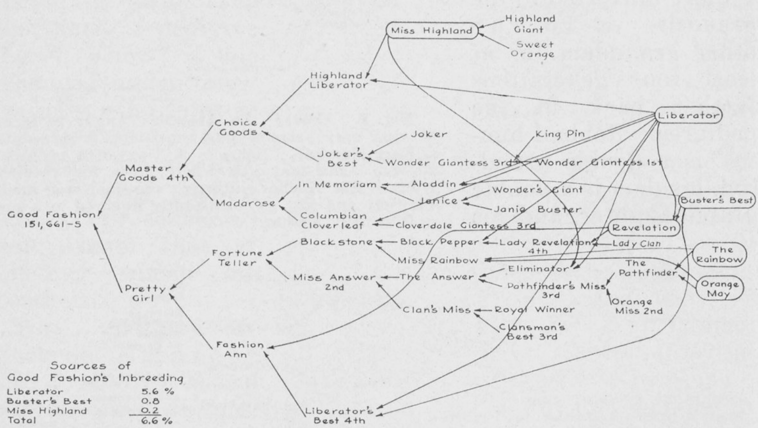

Fig. 10. A Poland China pedigree showing linebreeding consistent enough to keep the relationship to Liberator high, but so far back in the pedigree that the intensity of the inbreeding is very low.

The pedigree of the Hereford calf (fig. 11) shows extreme and deliberately planned linebreeding to Prince Domino, along with a tiny bit of linebreeding to Beau Aster. This pedigree comes as near to being pure linebreeding to one ancestor alone, as is often seen. Prince Domino dominates the pedigree. This calf (due to be born in the spring of 1933) probably will get about ¾ of its inheritance from Prince Domino and half of the rest from Beau Aster.

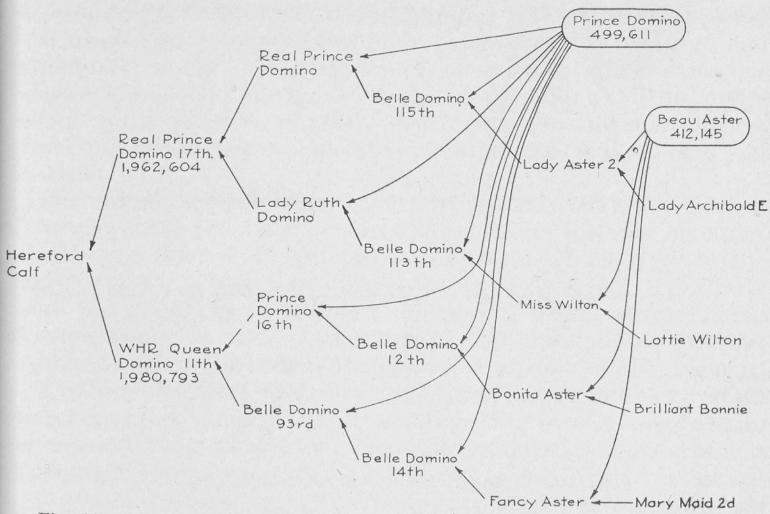

Fig. 11. Long-continued, extreme and deliberately planned linebreeding to Prince Domino, with a very little linebreeding also to Beau Aster. The total intensity is 29 percent, which is not very much more than that from one generation of parent-offspring mating. Yet the relationship to Prince Domino is held at 66 percent ("75 percent of his blood") and to Beau Aster at 11 percent.

VIOLENT INBREEDING AS A MEANS OF BREED IMPROVEMENT

The pedigrees (fig. 12) of Nathan (a Poland China from a University of Minnesota breeding experiment) and College Gleam 3d (a Duroc Jersey from the Iowa State College herd) cannot be called linebreeding since both are extraordinarily intense (59 percent and 50 percent, respectively) and each is directed at many different ancestors with no one ancestor predominating. They illustrate some of the most intensive inbreeding yet done with swine.

The evidence is reasonably clear that such extreme inbreeding cannot be kept under control of selection and will in the majority of lines lead to the fixation of undesired traits, perhaps even to the extinction of the line just as has been the case with the inbreeding of corn. It is possible, however, that recrossing the best lines which survive such inbreeding will produce animals superior to the original stock with which the inbreeding commenced, just as has been the case with the hybrid corn produced by crossing certain inbred lines. Or the highly inbred male used on nearly random bred females may sire offspring which are better individuals than those same dams would produce to sires which were not highly inbred. Such methods of alternating violent inbreeding and the accompanying selection with violent outcrossing are pointed toward the same goal as

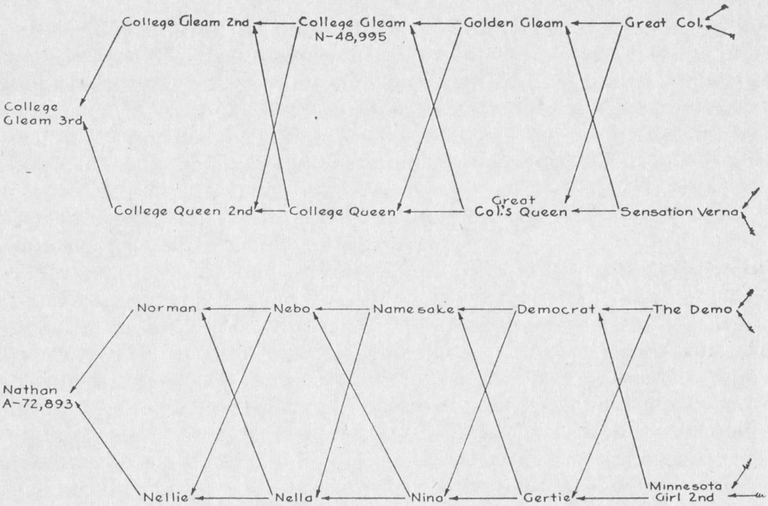

Fig. 12. Some actual examples of long-continued full brother x sister matings in swine.

the mild linebreeding and mild outcrossing methods which are the subject of this bulletin. The violent method is more wasteful of material but more economical of time than the linebreeding method. Since the animal breeder's material is more costly than the plant breeder's, the former has naturally not adopted the violent method as much as the plant breeder has. Which method is the sounder in the nation's economy in the long run depends mainly upon the effectiveness of selecting individual animals from among a nearly random-bred population as compared with the effectiveness of selecting between inbred lines. Experiment stations will no doubt continue to explore the possibilities of the violent method, even though it appears unlikely that such a method can be as well suited to animal material as it is to plant material.

GENETIC BASIS OF LINEBREEDING

Linebreeding has two genetic aspects. First, like any other system of partial isolation of different parts of the breed from each other, it promotes uniformity within groups and unlikeness between groups. This permits effective selection *between groups*. Breaking the population into uniform groups unlike each other is especially necessary if selection is to be effective for two kinds of traits: first, those (like fertility in swine) where the expression of the trait is so modified by environment both known and unknown, that mass selection for it is woefully weak and leads to many mistakes; and secondly, those traits dependent upon complex interactions of genes (''nicking'') of such a nature that the presence of some of the genes does not foreshadow at all clearly the kind of trait which will be manifested when all are present. Such complex interactions of genes do occur sometimes but perhaps are rather rare exceptions.

The second genetic aspect of linebreeding is that it makes more probable the recovery in one or more animals of somewhere near the same combination of traits which were in the ancestor toward which the linebreeding is directed. No doubt there are hundreds of units of inheritance which are not fixed (homozygous) in each farm animal. The number of different combinations of inheritance which each parent might transmit to any one offspring certainly runs far into the millions. With such enormous numbers of *possibilities*, the laws of *probability* have every opportunity to express themselves. Thus while it is theoretically *possible* for a grandson to have half his inheritance from one grandsire, it is so highly *improbable* that for all practical purposes one seeking to select from among even a very large number of grandsons and granddaughters those most like one of the grandsires in all his traits, would succeed in getting a group which would have only slightly more of their inheritance from that grandsire than the 25 percent which would be expected in the absence of selection. Linebreeding takes advantage of the laws of probability to hold the expected amount at about an equilibrium (instead of letting it be halved with each generation as would be the case if all the matings were outbreeding). Anything gained by selection is likewise held and further gains by future selections can be added to that already gained. It provides, so to speak, a ratchet mechanism for holding the gains already made by selection while attempting to make further gains. This is why selection can be more effective when combined with linebreeding than when practiced in an outbreeding system.

On account of the selection of the ancestors toward which the inbreeding is directed, the homozygosis produced by linebreeding is more apt to be for desired traits than is the case with undirected inbreeding. Otherwise linebreeding is no more effective in increasing homozygosis than are other forms of inbreeding which are equally intense.

APPENDIX

THE MEASURES OF INBREEDING AND RELATIONSHIP

Accurate measures of the probable likeness between the genotypes of two animals related by descent and of the probable extra homozygosis of an animal whose parents are related were first given by Wright.* The full formulae are:

The coefficient of inbreeding (F_X) of animal X is

$$F_X = \Sigma\left[\frac{1}{2}^{n+n'+1}(1+F_A)\right]$$

and the coefficient of relationship (R_{XY}) between animals X and Y is

$$R_{XY} = \frac{\Sigma\left[\frac{1}{2}^{n+n'}(1+F_A)\right]}{\sqrt{(1+F_X)(1+F_Y)}}$$

A is any ancestor of both sire and dam of X in the case of the inbreeding coefficient, or of both X and Y in the relationship coefficient. The number of generations from the sire of X in the case of the inbreeding coefficient, or from X in the relationship coefficient, back to the common ancestor A is n. Similarly n′ is the number of generations back from the dam of X in the case of the inbreeding coefficient, or from Y to the common ancestor A. Σ indicates that each such line of descent back to A in one line and down from A in another shall be figured separately and the separate answers shall be added together. In the case of the inbreeding coefficient, the total thus obtained is the probable proportion of the heterozygosis which was in the ancestors at the time to which the pedigree was traced but which has become fixed ("homozygous") in X. In the case of the relationship coefficient, it is the extra likeness (expressed as a coefficient of correlation) between the heredity of animal X and the heredity of animal Y over and above the average likeness among unrelated descendants from samples of ancestors out of the same population as those to which the pedigrees of X and Y were traced. The expression $(1 + F_A)$ takes into account the increased prepotency of inbred ancestors. The denominator $\sqrt{(1 + F_X)(1 + F_Y)}$ in the relationship coefficient allows for the well-known effect of inbreeding in increasing the variability of a whole population consisting of inbred but unrelated lines.

The only theoretical assumptions on which the formulae rest are that inheritance is Mendelian in the broad sense of that word and that the contributions of sire and dam are approximately equal. The comparatively unimportant case of sex-linkage where the contributions of the two parents are not equal is neglected.

Both measures express only the effects of relationship by descent. Whatever has been accomplished by selection or by assortative mating on the basis of external appearance or performance is not included. This is an exceedingly small omission so far as the coefficient of inbreeding goes and so far as the coefficient of relationship is used to express likeness when each pair of genes is considered by itself. It is an important omission if the coefficient of relationship is used to express

*Wright, Sewall. Coefficients of inbreeding and relationship. American Naturalist 56:330-338. 1922.

Wright, Sewall. Mendelian analysis of the pure breeds of livestock. I. The measurement of inbreeding and relationship. Jour. of Heredity 14:339-348. 1923.

the likeness between the animals, each considered as the sum total of all its parts. Systems of mating like individuals together regardless of pedigree can result in rather high likenesses between animals bred toward one outward ideal, although those animals, if not closely related, will have little likeness to each other, gene by gene, and almost no extra homozygosis.

Both measures express the result as compared with the population at the ancestral end of the pedigree. If the pedigrees are traced still further, additional inbreeding or relationship may be discovered but that is relative to a still earlier date. Thus the pedigree of Good Fashion shows all the linebreeding found if the pedigree is traced back to animals born in 1918 or just afterward. If all lines were traced to 1916 more linebreeding—perhaps as much as 1 or 2 percent more—would be found arising from the fact that Liberator's sire (The Clansman) is also an ancestor in several other lines of the pedigree. The figure shown is relative to the Poland China breed of 1918. The new figure would be relative to the Poland China breed of 1916. There is no real inconsistency here, although there is always the chance (as occurs in this case) of a small sampling error through stopping the pedigree just short of where it might have shown that the ancestors at the end of the lines were rather closely related to each other instead of being a representative sample of the whole breed.

It usually isn't worth while to examine pedigrees much farther back than four or five generations for inbreeding or relationship. Usually one can assume that the ancestors that far back were about a representative sample from among those of the breed then alive which succeeded in leaving descendants in the next generation. For example in a (still unpublished) study of the Holstein-Friesian breed we found that the average inbreeding of those born in 1909 was $4.7 \pm .5$ percent with an average random relationship to each other of $2.6 \pm .5$ percent both figures being relative to the foundation stock at about 1883. If we find that a present-day Holstein-Friesian animal is inbred 20 percent relative to 1909, it will be reasonably accurate to assume that this is a 20 percent decrease in the 95.3 percent of the 1883 heterozygosis still remaining in 1909. In other words, 20 percent relative to 1909 is probably about the same as 23.8 percent relative to 1883. Likewise if this Holstein-Friesian is related 40 percent to another, both pedigrees being traced only back to 1909, we are not likely to be seriously in error by assuming that if both were traced back to 1883 the relationship found would be about 41.6 percent (2.6 percent plus 40 percent of 97.4 percent).

EXACT COMPUTATION OF THE COEFFICIENTS

The pedigree of "E. M. Moore 26" will illustrate these computations on a moderately complicated pedigree. There are four different ancestors from which his sire and dam may have inherited the same gene in different lines. In all there are 13 different ways by which a gene may have come to E. M. Moore 26 through his sire and an exact duplicate of that gene may have come to him through his dam, thus making him homozygous for that gene. Those 13 different combinations of lines of descent are shown in fig. 13. From each combination there comes a certain probability that E. M. Moore 26 will be more homozygous than if his parents had not been related. The sum of these 13 separate probabilities is the probable proportion (inbreeding coefficient) of those genes which were heterozygous in the population from which his ancestors came, but which have become homozygous (fixed) in him. Nearly half of the total comes from the first line which is the only one to an ancestor which is itself inbred. No one of the last eight lines is important. They illustrate the general principle that relationship between

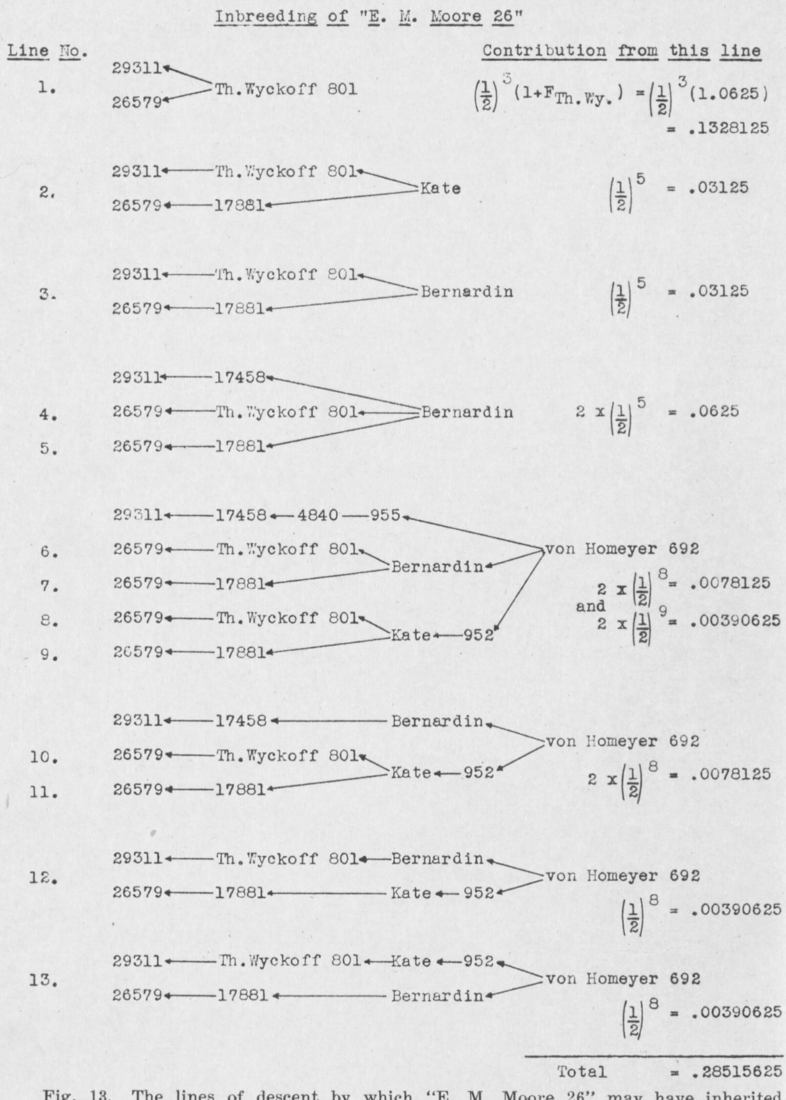

Fig. 13. The lines of descent by which "E. M. Moore 26" may have inherited identical genes from his sire and from his dam.

the sire and dam isn't likely to contribute much to the inbreeding intensity if it is only found far back in their pedigrees. The computations shown in fig. 13 are carried out to an absurd number of decimal places, merely to show the steps in the process. For practical purposes two places (or three at the most) would be quite far enough.

The relationship of E. M. Moore 26 to "Thomas Wyckoff 801" will illustrate the exact computation of the relationship coefficient. There are 10 different combinations of lines of descent through which E. M.

Relationship of E. M. Moore 26 to Thomas Wyckoff 801

Line No.		Contribution
1.	E.M.Moore 26 ← 29311 → Th.Wyckoff 801	
2.	E.M.Moore 26 ← 26579 ← Th.Wyckoff 801	$2 \times \left(\frac{1}{2}\right)^2 (1+F_{Th.Wy.})$ = .50 x 1.0625 = .53125
3.	E.M.Moore 26 ← 29311 ← 17458 ← Bernardin	
	Th.Wyckoff 801 ← Bernardin	
4.	E.M.Moore 26 ← 26579 ← 17881 ← Bernardin	$2 \times \left(\frac{1}{2}\right)^4$ = .125
	Th.Wyckoff 801 ← Kate	
5.	E.M.Moore 26 ← 26579 ← 17881 ← Kate	$\left(\frac{1}{2}\right)^4$ = .0625
6.	E.M.Moore 26 ← 29311 ← 17458 ← 4840 ← 955 ← von Homeyer	
	Th.Wyckoff 801 ← Bernardin ← von Homeyer	
7.	E.M.Moore 26 ← 26579 ← 17881 ← Kate ← 952 ← von Homeyer	$2 \times \left(\frac{1}{2}\right)^7$ = .015625
8.	E.M.Moore 26 ← 29311 ← 17458 ← 4840 ← 955 ← von Homeyer	
9.	E.M.Moore 26 ← 29311 ← 17458 ← Bernardin ← von Homeyer	
10.	E.M.Moore 26 ← 26579 ← 17881 ← Bernardin ← von Homeyer	
	Th.Wyckoff 801 ← Kate ← 952 ← von Homeyer	$\left(\frac{1}{2}\right)^8 + 2 \times \left(\frac{1}{2}\right)^7$ = .01953125
		Total = .75390625
		$\sqrt{1.2852 \times 1.0625}$
		= 64.5%

Fig. 14. The lines of descent by which "E. M. Moore 26" and "Thomas Wyckoff 801" may have come to possess identical genes.

Moore 26 and Thomas Wyckoff 801 may have come to possess identical genes. Those are shown in fig. 14. The first two lines are of direct descent and correspond to the "percentage of blood" calculations familiar to most breeders, except that there is included here a small correction to take into account the extra prepotency of Thomas Wyckoff 801 on account of his inbreeding. Lines 3, 4 and 5 show collateral relationship of considerable importance. The last five lines make very small contributions and illustrate again the general principle that relationship which doesn't show in the first few generations of the pedigrees isn't likely to be important.

APPROXIMATE MEASURES FOR PRACTICAL USE

The coefficient of relationship is identical with the ordinary "percentage of blood" method, provided (1) both ancestor and descendant are not inbred or are inbred with the same intensity and (2) their whole relationship comes about because one is the descendant of the other, with none of it coming because both are descendants of other ancestors through different lines.

Where the descendant is more highly inbred than the ancestor, the resemblance between them is a little less, in accordance with the well-known tendency of inbreeding to uncover traits not seen in the immediate ancestors. Where the ancestor is more highly inbred, the resemblance between them will usually be a little more than the "percentage of blood" figure indicates, in accordance with the well-known fact that inbred ancestors are more prepotent than outbred ones. But in pedigrees usually encountered in actual practice, ancestor and descendant don't differ enough in intensity of inbreeding to make this important.

Provision No. 2 is not so easily met. Y (in the pedigree on page 341) has "50 percent of the blood of K" but, in addition to that, K is an uncle of Y through being a half brother of Y's dam, L. This makes Y and K more alike than ordinary parent and offspring. The simplest way to figure this collateral relationship through common descent from M is to calculate what percentage of M's blood K has and what percentage of M's blood Y has, not counting that which comes to Y through K, and then to *multiply these two percentages together.* Thus 50 percent of the blood of M in K times 25 percent of M's blood in Y through other ancestors than K makes 12½ percent resemblance between Y and K through common descent from M. Added to the 50 percent of direct relationship from K to Y, this makes a total relationship of 62½ percent between K and Y. Since Y is more intensely bred than K this is reduced to 59 percent, if the small correction for the difference in intensity of inbreeding is thought worth making.

The general rule for figuring relationship is: First, figure the relationship by direct descent as is done in the ordinary "percentage of blood" method in which a parent counts 50 percent, a grandparent 25 percent, a great grandparent 12½ percent, etc., the importance of each ancestor being halved with each additional generation it is back in the pedigree. Second, *separately for each ancestor* through which there is collateral relationship calculate the percentage of that ancestor's blood which is in each of the two animals whose relationship to each other is to be found, being careful not to include any which has already been counted in the direct relationship. Multiply these two percentages together and add the product to the direct relationship.

It is important to make the "percentage of blood" calculation separately for each ancestor. A and B (on page 341) have "100 percent of common blood," but this tells little about how nearly alike they are. "Percentage of common blood" is almost useless as a measure of relationship because likeness depends also on how far back into the pedigree one must go to find the common ancestors. A and B each have 25 percent of the blood of G. Twenty-five percent of 25 percent is 6¼ percent of likeness due to descent from G. There is another 6¼ percent of resemblance from descent from each of H, I and J.

The intensity of the inbreeding in any mating is one-half or a little more than one-half of the relationship between the mated animals. This is the best estimate of the danger in making any mating, although the danger depends not only on the intensity but also on whether the ancestor toward which the inbreeding is directed, had more or less than the usual amount of undesirable (perhaps hidden) inheritance.